OBSERVATIONS ON THE FOOD REACTIONS OF ACTINOPHRYS SOL.

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INTRODUCTION.

Observations on the ability of the protozoa to choose their food date back to 1838 at least. At that time Ehrenberg observed that various organisms ingest carmine which, as food, is nothing more than inert matter. From 1838 until 1902 most of the workers in this field held that protozoa do not possess the power of choosing their food. Even at the present time, as stated by Visscher ('23) in the introductory to his work on *Dileptus gigas*, it is evident that the selection of food has thus far been positively demonstrated in a very few forms.

Kepner and Whitlock ('21), in their work on Amwba, give proot of qualitative efforts on the part of Amwba to meet certain contingencies. Up to the present time proof of such qualitative effort in other rhizopods has not been recorded so far as I have been able to determine.

This work was done under the direction of Professor William A. Kepner, to whom I am deeply indebted for helpful suggestions regarding these experiments and the preparation of this paper. I am also indebted to Professor Bruce D. Reynolds for valuable criticisms and suggestions.

CULTURE METHOD.

The best cultures were obtained in an infusion made by boiling three grains of wheat for five minutes in 100 cc. of filtered spring water. The infusion, along with the three grains of boiled wheat, was placed in a small, clean, glass aquarium and allowed to stand at least twenty-four hours before the animal was introduced. After about a month had passed *Actinophrys* could be secured

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from such a culture usually in abundance. The cultures were kept covered with thin sheets of plate glass and were kept in the darkest portion of a well lighted room. To keep the cultures going it was found necessary to add to each culture 5 to 10 cc. of boiled spring water per week. The Heliozoa subsisted chiefly upon *Peranema* and *Colpidia*, the progenitors of which were introduced when the cultures were inoculated.

METHODS OF OBSERVATIONS.

All observations were made under the compound microscope—the 4 mm. objective and number 10 eyepiece being used in practically every observation made. A number 10 eyepiece containing a corrected micrometer, and having a camera lucida attached was kept at hand in case sketches or measurements were to be made.

Cultures in Petri dishes were examined under the 16 mm. objective. In this way observations were obtained on movement and general behavior in a habitat to which the animals were thoroughly accustomed.

A few observations were made on specimens in a drop of water on an ordinary micro-slide under a cover glass, but most observations were made on specimens mounted in a hanging drop. The former method is inconvenient because water has to be supplied to compensate for evaporation. This often disturbed the Actinophrys in such a way as to cause it to lie quietly for some time, hence, much valuable time may be lost. The hanging drop method alleviated this trouble once the mount was properly made. To prepare the mounts, first a glass ring about I cm. in height and 1½ cm. in diameter, was placed on a clean slide and attached thereon by applying vaseline around the proximal end of the ring. The ring was then supplied with well-oxygenated water until the meniscus came up to half the height of the ring. Clear water in which Elodea or Chara was actively growing was found to be best. The supply of oxygen in the water in the ring tends to replenish the supply in the hanging drop as it is used up by the mounted Actinophrys sols. The desired number of the above mentioned specimens was then isolated by means of a capillary pipette and placed on a clean number one coverglass. Next, with another capillary pipette, the desired objects of prey were applied to the drop on the coverglass containing Actinophrys sol. The upper end of the ring, which had previously been prepared, was smeared with a small amount of vaseline. The coverglass was then inverted and gently pressed down on the ring. Mounts, prepared as described above, often lasted two weeks for observation. In observing these mounts under the 4 mm. objective, better lighting was obtained by removing the sub-stage condenser and employing the concave mirror.

Special Pseudopods.

The special pseudopods for taking in prey are always composed of hyaline ectoplasm. There are three general types of these special pseudopods. First, if the object to be ingested is very small and relatively motionless, a small, straight pseudopod is extended, and upon coming in contact with the object spreads out into a cup which encircles and closes in closely on the object. These pseudopods often resemble a dipper if the protruding end happens to pass beyond the food object before contact is made. Second, if the motionless object be large, a wide, hyaline outgrowth (Fig. I, I a) of protoplasm advances towards the prey. When it gets quite near to, or comes in contact with the prey, the tip of this special pseudopod expands in all directions laterally. These lateral expansions close about the large motionless food object usually in close contact with it. In the few instances when close contact may not be made about the large motionless food object, the food vacuole is always decidedly smaller than is the case with animate objects mentioned in the next or third class. Third, large sacklike pseudopods (Fig. 2, 1 a) are sent out to encircle active animals. The victim is often cut off from a means of escape by a palisade of rays on one side, and by the approaching special pseudopod on the other.

REACTIONS TO INANIMATE OBJECTS.

In experiments on reaction to inanimate objects, only such materials were used that were thought to be non-toxic to *Actinophrys*. In addition, the materials chosen were of such nature as to be easily distinguishable in the vacuoles. The following were tried:

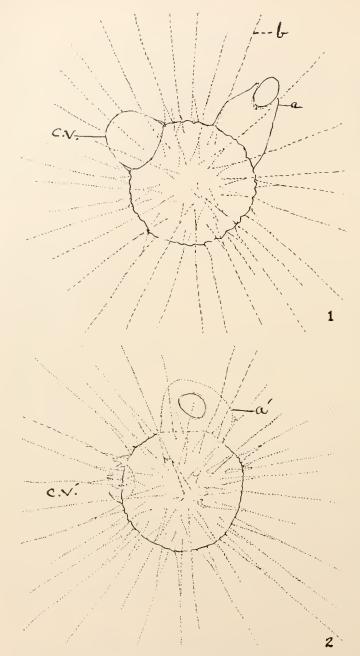


Fig. 1. Sketches illustrating the ingestion of an inanimate object—granule of wheat starch.

- 1. Actinophrys sol with the granule partially enclosed by the foodgetting pseudopod, a; b, ray; c.v., contractile vacuole.
- 2. Same specimen one half hour later in which a has grown to a'. c.v.', Protoplasmic projections representing broken wall of emptied contractile vacuole. (\times 825.)

carmine, alizarine, powdered glass, plain wheat flour, corn starch, and powdered graphite. Ten experiments were tried with each of these materials, but evidence of ingestion was seen only in the experiments where carmine, wheat flour, and corn starch were used. In the experiments with each material care was taken to try individuals which were in different physiological conditions; c.g., small, underfed specimens, well fed specimens, and specimens which were accustomed to different types of food. Only experiments with materials which Actinophrys ingested will be recorded in this paper. The following tables contain the results:

TABLE I.

REACTIONS TO CARMINE.

Experiment.	No. of Indi- viduals in Hanging Drop.	No. which Did Not Take Any Particles within 2 Hrs.	No. Taking Only One Particle within 2 Hrs.	No. Taking Two Parti- cles within 2 Hrs.	No. Taking Three Particles within 2 Hrs.	No. Taking More than Three Particles within 2 Hrs.
1	8	5	2	I	0	0
2	5	4	I	0	0	0
3	II	9	I	I	0	0
4	7	5	I	0	I	0
5	4	3	I	0	0	0
6	5	3	2	0	0	0
7	6	5	0	I	0	0
8	3	2	I	0	0	0
9	15	I 2	2	I	0	0
10	5	4	I	0	0	0
Total	69	52	12	4	1	0
Per cent		75.4	17.4	5.8	1.4	0

In each experiment observations were made as soon as the hanging drop mount was made, then every fifteen minutes thereafter for a period of two hours. In no case did it seem probable that ingestion followed by egestion took place within the time between observations. This is because *Actinophrys* reacts slowly.

Table I. shows that fifty-two individuals (75.4 per cent.) did not take carmine at all. Twelve individuals (17.4 per cent.) took only one particle of carmine. The number taking two particles was four, only one individual took as many as three particles, while none took more than three. Hence, it is evident that car-

mine was ingested by only about one fifth of the total number of individuals, and these took carmine in relatively small quantities.

I was fortunate in seeing eight of the specimens ingest the particles. In each case small, straight, food-getting pseudopods were extended and the particles were closely embraced. This phenomenon will be referred to again later.

TABLE II.

REACTIONS TO WHEAT FLOUR.

Experiment.	No. of Indi- viduals in Hanging Drop.	No. which Did Not Take Any Particles within 2 Hrs.	No. Taking Only One Particle within 2 Hrs.	No. Taking Two Parti- cles within 2 Hrs.	No. Taking Three Particles within 2 Hrs.	No. Taking More than Three Particles within 2 Hrs.
I	5	2	I	2	0	0
2	5	3	2	0	0	0
3	7	4	2	0	I	0
4	4	2	1	0	0	I
5	9	5	3	I	0	I
6	7	6	0	I	0	0
7	10	7	2	0	I	0
8	3	2	I	0	0	0
9	6	3	2	I	0	0
10	8	5	2	I	0	0
Total	64	39	16	6	2	2
Per cent	_	61	25	9.3	2.3	2.3

In Table II. are found the results of ten experiments with plain wheat flour. Thirty-nine individuals (61 per cent.) did not ingest particles of the flour. Twenty-five per cent. ingested only one granule each, and three tenths per cent. ingested two granules, while two and three tenths per cent. ingested three and four granules, respectively. None were observed to take in more than four granules.

The experiments with flour were carried out under practically the same conditions as the experiments with carmine. However, the results of the former tend to show that particles of wheat flour are taken in by a larger number of individuals, and in relatively larger amounts, than carmine was by individuals under similar conditions. This can probably be explained by the fact that particles of wheat flour may be coated with a thin film of protein material which *Actinophrys* is able to digest and assimilate,

though I was not able to detect any change in granules which lay in the food vacuoles for as long as five days.

The type of pseudopod employed in engulfing particles of wheat flour belongs to the second class previously described for the taking in of relatively large motionless objects. As with the carmine particles, the pseudopod closely embraces the particles of flour, though the process is very much slower. The slowness of ingestion is probably due to the larger size of the particles.

Table III. contains the results of ten experiments with corn starch. Fifty-eight individuals (85.3 per cent.) did not take in granules at all. Eleven and seven tenths per cent. engulfed only one particle each. Three per cent. took in two particles each,

TABLE III.

REACTIONS TO CORN STARCH.

Experiment.	No. of Individuals in Hanging Drop.	No. which Did Not Take Any Particles within 2 Hrs.	No. Taking Only One Particle within 2 Hrs.	No. Taking Two Parti- cles within 2 Hrs.	No. Taking Three Particles within 2 Hrs.	No. Taking More than Three Particles within 2 Hrs.
I	12	10	2	0	0	0
2	8	8	0	0	0	0
3	5	4	0	I	0	0
4	9	7	I	1	0	0
5	9	8	I	0	0	0
6	3	3	0	0	0	0
7	6	5	I	0	0	0
8	5	3	2	0	0	0
9	5	4	I	0	0	0
ΙΟ	6	6	0	0	0	0
Total	68	58	8	2	0	0
Per cent	_	85.3	11.7	3	0	0

while none took in more than that number. By referring to Tables I., II., and III., it may be easily seen that these results show that corn starch was taken in by fewer individuals than either carmine or wheat flour.

The method of ingesting corn starch was observed to be practically identical with the method referred to under experiments with wheat flour, viz., inanimate particles are closely embraced by the food-getting pseudopods.

Since it is more convenient to merely state the results of the

following experiments, tables will not be given. In all experiments the procedure as outlined under the reactions to inanimate objects was followed and the data were obtained in a corresponding manner.

REACTIONS TO MOTIONLESS ANIMATE OBJECTS.

Under this heading reactions to living yeast, motionless algæ, and *Euglena* cysts are recorded.

A. Desmids.

a. Scenedesmus.—In experiments with Scenedesmus forty-eight Actinophrys were involved. Sixty per cent. did not take the algæ. Those engulfing only one mass constitute thirty and three tenths per cent. The remaining nine and six tenths per cent. of the individuals engulfed two masses each. These desmids were taken in by the same type of pseudopod as were the inanimate objects.

b. A Larger, Desmid.—Fifty animals involved in ten experiments were tried with this desmid. Only four per cent. attempted to engulf the larger algae, and in one case only was the attempt successfull. In this case one Actinophrys sent out a pseudopod and partially surrounded the plant but was not large enough to completely surround it. This animal, while attempting to surround the desmid, was joined by another animal. This union appeared to be a complete fusion of the cytoplasm of one with that of the other, the nuclei remaining separate. After this fusion the pseudopod of the first animal was enlarged to completely surround the desmid. The desmid remained in the food vacuole of the multiple individual for a period of five hours and was then slowly forced out through the outer membrane. Nothing remained of the plant except the cellulose wall and a few particles which remained on the inside of it. A similar phenomenon in the Rhizopods was referred to by Delage and Herouard ('96), as a "Societe de Consumation." Distaso ('08) called attention to the grouping of A sol for the capture of large food objects.

B. Yeast.

In experiments with yeast seventy-two animals were used. Twenty per cent. of these took in one or more of the plants. Since yeast plants are so small it was impossible to keep check on the number taken in. When taking in objects of the above kind the pseudopod was of the small straight type referred to previously in this paper. The plants in all cases observed were closely embraced by the pseudopod until digestive fluid began to collect around them, filling a space between the outside of the plants and the wall of the vacuole.

C. Cysts of Alga.

Euglena cysts and cysts of Chlamydomonas were taken in in practically the same proportion. In each case one cyst each was taken in by fifteen individuals (20 per cent.). Four per cent. took in two cysts each, while only one per cent. ingested three each. There were not any taking in more than three cysts. The close embrace was employed in all ingestions observed.

The experiments with motionless animate objects show that *Scenedesmus* is taken more often than either living yeast, *Euglena* cysts, or cysts of *Chlamydomonas*; also, that a larger desmid was rarely chosen as an object of food. The ingestion of the larger algae required the cooperation of two or more individuals.

REACTIONS TO MOVING ANIMATE OBJECTS.

In reacting to moving animate objects *Actinophrys* presents an entirely different type of food-getting pseudopod. Previously, this was referred to as a relatively large, cup-like pseudopod. Instead of the close embrace of the object by the pseudopod, which was referred to under reactions to inanimate objects, we have what may be referred to as a "subtle embrace." A description of the capture and ingestion of a *Colpidium* will serve to make clear what is meant by a "subtle embrace."

While watching the movements of an Actinophrys a Colpidium was observed to encounter the tips of some of the rays of the former. The Colpidium became motionless almost instantly, as if completely paralyzed by the encountered rays. While watching to see the ultimate fate of the ciliate a relatively large mass of cytoplasm was observed to be protruding from the surface of the Actinophrys. This mass, which proved to be a food-getting pseudopod, came forward as a single mass until it was four micra

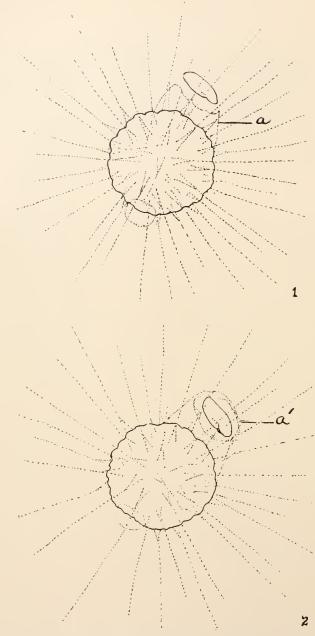


Fig. 2. Sketches illustrating the ingestion of a moving animate object— Chilomonas.

- 1. Actinophrys sol with a pseudopod, the contour of which is becoming adapted to that of the prey before coming into contact with the latter. a, food-getting pseudopod.
- 2. Same specimen fifteen minutes later. a has grown to become a', which shows wide detour about the motile prey. $(\times 750.)$

away from the quiet *Colpidium*; then, without approaching farther. it gave off two branches (Fig. 2, 1 a). These branches continued to protrude, encircling the victim, and fusing on the opposite side of it. Thus far, the Colpidium was not approached closer than two micra by the branches of the engulfing pseudopod. Hence, the pseudopods were thrown subtly, but not intimately, around the prey. Immediately after the fusion of the pseudopods beyond the prey they spread in such a way as to form a hollow sphere or vacuole containing the Colpidium on the inside (Fig. 2, 2). The vacuole then contracted around the prey, which in the meantime became stimulated to exhibit frantic efforts, apparently for the purpose of escape. These efforts were kept up for a period of at least five minutes before the imprisoned animal finally became quiet again. The vacuole containing the prey was eventually incorporated into the body and grew smaller as digestion proceeded, and disappeared completely when the indigestible particles were finally ejected through the cell membrane of Actinophrys.

A. Ciliates.

Colpidium.—Ten experiments with Colpidia reveal the fact that forty individuals (50 per cent) took in one or more Colpidia. Thirty-seven and seven tenths per cent. engulfed one Colpidium each. Twelve per cent. took in two specimens each; while only three tenths per cent. engulfed three each. Apparently, the reason why there was such a small per cent. taking in as high as three each lies in the fact that Colpidium is relatively too large to be engulfed in larger numbers by Actinophrys within two hours.

Loxocephalus granulosus.—Loxocephalus is taken in very readily and in relatively large numbers by Actinophrys. In the experiments with the above mentioned ciliate only thirty-six (40 per cent) of the Heliozoans failed to ingest one or more. Thirty per cent. of the individuals engulfed one ciliate each. Two each were taken in by twenty per cent., while ten per cent. were observed to have three vacuoles containing one Loxocephalus each. The type of pseudopod used in taking in this organism was observed to be practically identical with the type described under reactions to Colpidium.

Stylonychia mytilus.—This ciliate is much larger and stronger

than Actinophrys. Some of the cilia have been modified to form bristle-like cirri which may be used as organs of offence, or defence. Hence, it is hardly possible for Actinophrys to capture such an organism single-handed, and so far as known no one has ever observed such. I have seen four different cases where individual Stylonychia were engulfed by a group of Actinophrys. These groups in two cases were assembled after one Actinophrys sol had tried to capture and ingest the larger and stronger animal. In the other two cases the groups had been previously formed. In no case was a Stylonychia taken in by a group of less than four individuals. The group action here, if it may be called group action, differs in at least one respect from the association of individuals described by Kepner ('25). In the case he reported, three individuals united to take in a motionless desmid, and the pseudopods of the former embraced the latter closely. In the case of a group taking in a Stylonychia the pseudopods presented the phenomenon of the loose, or subtle embrace described under reactions to Colpidium.

Other Ciliates.—Ten experiments were carried out with Frontonia lucas, Nassula ornata, and Spirostomum ambiguum respectively. Some of the experiments in each case were kept under observation for five days. However, in no case were any of the above-mentioned ciliates engulfed by Actinophrys; while Colpidia and Chilomonads, which happened to be among these ciliates, were all engulfed sooner or later. This certainly indicated a definite discrimination in regard to the type of ciliate taken in. On what is this discrimination based? Whatever the basis, it is hard to believe that either Frontonia, Nassula or Spyrostomum would be more difficult, from a mere physical standpoint, to capture and engulf than Stylonychia.

B. Reactions to Flagellates.

Chilomonas paramecium.—Reactions to this flagellate were practically the same as described under reaction to the ciliate, Colpidium. Forty-one individuals (51 per cent.) of Actinophrys soldid not engulf Chilomonas. Of the remaining forty-nine per cent. forty per cent. engulfed one each. Six per cent. took in four each. Peranema trichophorum.—Peranema proved to be engulfed

very readily by Actinophrys. Only twenty-five individuals (42 per cent.) failed to take in this flagellate. Thirty-five per cent. engulfed one per individual. Nineteen and one tenth per cent. took in two each, and three per cent. three each. In no case were as many as four Peranema engulfed by an individual. The complete process of capture and ingestion was observed in eleven cases. In each the subtle embrace was employed.

Euglena viridis.—Euglena viridis was taken more readily than any other food material. Thirty-five individuals (58.4 per cent.) of the Heliozoan ingested one each. Ten per cent. took in two each, and one per cent. three each.

Euglena, as a rule, was embraced more closely than either of the other moving animate objects. I have not been able to observe definitely why this was the case. However, this deviation from the usual procedure in ingestion of moving animate objects probably has some connection with the fact that Euglena was often brought in contact through a reaction with the body proper of Actinophrys before a food-getting pseudopod was sent out. This contact with the body proper was brought about by a sudden jump of Euglena in the direction of the body proper of Actinophrys while reacting to a contact with the rays. The exact reason for this sudden jump on the part of Euglena has not been determined, though it has been suggested that the long flagellum of Euglena became attached to the body of Actinophrys, probably, by a mucilaginous property of the latter. Then in an effort to free itself, the Euglena pulled itself into contact with the body of Actinophrys to which the end of its flagella was fixed. Thus the body of the flagellate became fastened by the same property. If this be true, the food-getting pseudopod which arises from the outer region of the Heliozoan's body, would quite probably adhere closely to the flagellate's body as it encircled it. Should, however, the Euglena begin to squirm, the cup of the pseudopod would open up to form a larger cavity around the victim. Thus in case the Euglena began to struggle, what was started as a close embrace was forthwith transformed into a subtle embrace.

D. Reactions to Rotifers.

Only individuals belonging to one or two of the small species of Rotifers were taken in by Actinophrys. Rotifers are the only

multicellular animals which were observed to be captured and ingested by the Heliozoan. Here, as with Stylonichia, a group of less than four was not strong enough to capture a Rotifer. I was fortunate to see the complete struggle involved in the capture and ingestion of five specimens by five different groups of Actinophrys. Here, as in the case of the capture and taking in of Stylonychia, some of the groups were formed after a single individual had become attached to the prey (Fig. 3). In the formation of two of these groups individuals which were entirely out of the low power field of the microscope joined the fray, fusing with their comrades which were already involved. In one of the above mentioned cases four individuals were not in the field when the Rotifer was encountered by an Actinophrys which was in the field. In the other case, likewise, three were outside of the field of vision. In these cases the rays of the individuals which came into the field of the microscope to join in the feast were not adjacent with the rays of those already involved. This seemed to indicate that there must be some way of sending out a call for assistance when the object was too large and pugnacious to be conquered and swallowed by one individual. The reason that it cannot be said definitely that this is the case is because the outsiders might be drawn in by currents set up in the medium by the floundering of the attacked prey. The fact that a number of Actinophrys sol fused to form an aggregate when brought together by agitating the surrounding medium with a glass filament, strengthens the above mentioned idea. Whatever may be the cause of the formation of temporary colonies, the phenomenon is, at least, of interest. By virtue of this fact, it becomes easier to conceive of how multicellular animals may have arisen by the association and cooperation of individual cells. Be this as it may, the formation of multiple individuals by Actinophrys sol makes possible the capture and ingestion of larger objects of prey. This is essentially in agreement with Distaso's ('08) observations on A. sol. Apparently this temporary colony formation also serves a protective rôle. It is probably of interest to note that an animal so low in the scale of organic life exhibits the phenomenon of coöperation in the fundamental activities of its life.

By comparing the results of the experiments carried out with

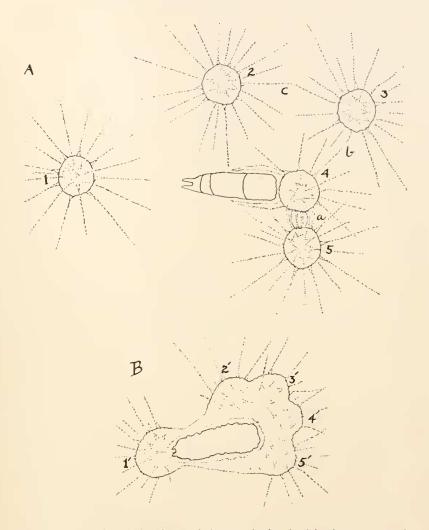


Fig. 3. A. Five Actinophrys sols later to be involved in the capture and ingestion of a rotifer. Specimens 4 and 5 already show advanced cooperation, a. Specimens 3 and 4 show the inception of coöperation through the fusion of two of their slender rays, b. Specimens 2 and 3 are also involved in the coöperation through the fusion of two rays at c. Specimen 1 is yet independent.

B. Same group showing progress made within two hours. Complete ingestion has been accomplished and some digestion has ensued. I', 2', 3', 4', and 5' shows the position taken by 1, 2, 3, 4, and 5, respectively, of Fig. 3 A. $(\times 260.)$

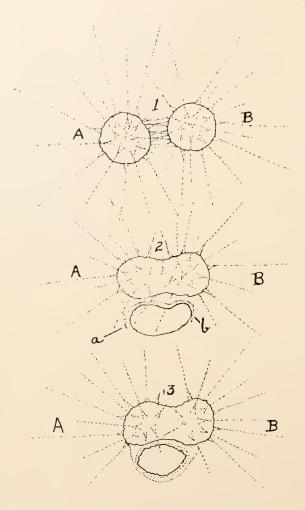


Fig. 4. Sketches illustrating the fusion, also, the cooperation of two *Actinophrys sols* in the capture and ingestion of a *Colpidium*.

- 1. Pseudopodial fusion in the union of the two individuals.
- 2. Coöperation of the same two individuals in ingestion of Colpidium by one individual, A, sending out a and individual B sending out b to form in common one large food-engulfing pseudopod.
- 3. Same specimens one and one half hour later. Prey engulfed by fusion of pseudopods a and b about it. $(\times 325.)$

the various types of objects it may easily be seen that Actinophrys sol feeds chiefly on the smaller ciliates and on the flagellates. The experiments with moving animate objects show that certain of these objects are eaten more readily and in greater numbers than are others. Difference in the size and vigor of the different food objects, no doubt, plays an important rôle in causing this discrimination. However, it is not probable that difference in size and vigor alone is the only factor causing the discrimination noted. The experiments with moving animate objects also show that such objects are not embraced intimately by the food-getting pseudopods of Actinophrys sol; but on the contrary, the moving animate objects, as a rule, are loosely or subtly embraced by the food-getting pseudopods.

SUMMARY.

- I. Actinophrys sol is essentially omnivorous.
- 2. Certain inanimate objects are ingested more often than others. Some inanimate objects apparently are not ingested at all.
- 3. Motionless animate objects are accepted, but not in appreciably greater numbers than inanimate objects.
- 4. Many free-swimming ciliates and flagellates are readily eaten, but certain ciliates apparently are not taken.
- 5. A degree of selection or discrimination was exercised between different food objects in every class of materials used.
- 6. Large objects of prey may be taken in by temporary colonies of *Actinophrys sol* which are formed for the purpose of taking in such objects.
- 7. As a rule, motionless animate objects and inanimate objects are closely embraced by the ingesting pseudopod; objects which struggle while being ingested are subtly embraced.

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